

Morphogenetic responses of *Populus alba* L. under salt stress

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Abstract: The morphogenetic responses to salt stress of Tunisian *Populus alba* clones were studied in order to promote their plantation in damaged saline areas. One year-old plants of three *P. alba* clones (MA-104, MA-195 and OG) were subjected to progressive salt stress by irrigation during two consecutive years. The plants were grown in a nursery, inside plastic receptacles containing sandy soil and were irrigated with tap water (control) or 3–6 g/l NaCl solution. During this study, leaf epinasty, elongation rate, vigor, internode length, plant architecture, and number of buds were evaluated. Test clone response was highly dependent on the applied treatment and degree of accommodation. The most pronounced alterations were induced under 6g/l of NaCl treatment including leaf epinasty, leaf elongation rate delay, vigor decrease, internode length shortening, and morphogenetic modifications. These responses were less noticeable in the MA-104 clone with respect to the two other clones. The salt effect induced a delay in the leaf elongation rate on the MA-195 and OG clones leading to an early leaf maturity. The vigour and internode length of the MA-104 clone was less affected than the other clones. The OG clone was the most salt-sensitive thus, it developed shorter branches and more buds number than MA-195 and MA-104. The effect of long-term salt stress was to induce early flowering of the *P. alba* clones which suggests that mechanism of salt accommodation could be developed.

Keywords: Poplar, salinity, leaf elongation, vigor, internode length, floral bud

Introduction

In Tunisia, the lack of summer rainfall, high evaporative demand, and high salinity of irrigation water has caused salt to accumulate in the soil. Such accumulation has been increased in some areas, the result of inadequate irrigation practices and lack of suitable

leaching, which raised water levels bringing salts to the soil surface. Saline and waterlogged areas covered respectively 12% (Mashali et al. 2005) and 10% of the country total area (Béjaoui et al. 2008), making rehabilitation of these areas complex and expensive (FAO 2005). Using fast-growing woody species such as *Populus* sp., which is known to tolerate salinity (Marcar et al. 1993) and has higher water consumption, might be an opportunity to phytoremediate such areas and, in the mean time, could decrease water levels.

The genus *Populus* is widespread in the Mediterranean, Central Europe, and the Middle East. By comparing the response of different *P. alba* and *P. nigra* clones to increasing levels of salinity, Abassi et al. (2004) showed encouraging tolerance degree of *P. alba* but with great variability among the clones. Furthermore, Sixto et al. (2005) pointed out that Spanish genotypes of *P. alba* showed an intermediate degree of tolerance to salinity between the one displayed by *Populus euphratica*, known as the most tolerant poplar species (Chen et al. 2003), and the one displayed by an hybrid of *P. euramericana* and *P. deltoides* × *P. alba* clones. Given the high variability of *P. alba* clones, a better understanding of morphological responses to salt stress is required before their utilization in degraded saline sites.

Plants growing in saline soils encounter osmotic stress and ion imbalance or disturbance in ion homeostasis and toxicity (Hu et al. 2005). Changes in water status can lead to reduce initial growth and limit plant productivity (Parida and Das 2005). The immediate response to salt stress is the moderate reduction to cessation of leaf surface expansion as salt concentration rises (Wang and Nil 2000) and petiole epinasty (El Iklil et al. 2000). After longer period of salt stress, detrimental effects are induced at the plant morphology, such as shortening internode length (Gucci et al. 1997; Barhoumi et al. 2007) and plant stunting (Takemura et al. 2002). Moreover, studies show that abiotic stress induced early-flowering of a *Populus* genotype (Meilan et al. 2004).

The overall goal of this study is to define the adaptive mechanisms developed by Tunisian *P. alba* clones in response to long-term salt stress through induced morphogenetic modifications. Three clones, different in terms of their tolerance to salinity, were compared by measurement of leaf expansion rate and epinasty, as well as, morphogenetic traits.

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Materials and methods

Plant material

Experiments were conducted in a naturally illuminated nursery at the National Institute of Research on Rural Engineering, Water, and Forests (Tunis, Tunisia), in a semi-arid to mild winter bioclimatic zone at 36°50' N, 10°14' E, 3 m of altitude, 475 mm annual average rainfall, 2952 hours/year of sunlight and 7.2–34.8°C of monthly average temperature. Three *Populus alba* L. var. *Hichkeliana* (Dode) Marie clones (OG, MA-195 and MA-104) known to show variability in their tolerance to salinity (Abassi et al. 2004), were grown in semi-controlled conditions. Poplar cuttings of 25 cm in height and 2 cm in diameter, taken in the winter, were planted in free-draining plastic pots (45 cm depth × 30 cm diameter) that contain coarse river sand as substratum. They were irrigated weekly for one year with half-strength Hoagland's solution (Fung et al. 1998). The experimental design was a split-plot with four replications. Clones were assigned to the main plot and water regime (control and salt stress) to the split plots. The latter consisted of 12 plants per plot and the total number of plants evaluated was 144.

Salt treatment

The salt stress experiment was carried out over two years (2010–2011). The 1-year rooted plants were divided into three treatments: control and two salt treatments (3 and 6 g/L NaCl). The control plants and the salt-treated ones were irrigated with half strength Hoagland solution. The NaCl concentration started from 3 g/L NaCl and increased stepwise by weekly 1 g/L NaCl steps until reaching 6 g/L NaCl. The salinity in the soil was monitored periodically by measuring the electrical conductivity in the drain solution using a WTW Cellox 325.

Morphology measurements were taken from May to September to determine the second-year vegetative growth of the *P. alba* clones.

The length of the newly emergent leaves of the plant apex was measured at three-day intervals with three replications of four plants per clone at each treatment level. Leaf length was measured with a digital caliper rule (0–150 mm, with a technical error of 0.01 mm) from the appearance of leaf shoots until their length stopped changing. The difference between the initial and the final measurement is expressed as the leaf elongation rate (mm·day⁻¹).

Epinasty was assessed as the change in the angle formed by the petiole and the main stem axis. It was measured at 3-day intervals with a transparent protractor on the 2nd, 3rd, and 4th mature leaf at the median part of the plant. Epinasty is estimated by the following formula: $E = A_s - A_c$, where A_s and A_c are the angles of stressed and control plants, respectively.

The plant architectural analysis is a morphogenetic approach: in this study, the traits analyzed included the branching system, vigor indices, and the mean length of both branches and inter-

nodes. The tree-branching system is characterized by branching orders or levels. An axis is defined as a topological structure developed on another one (apparition of a new structure). The position of one axis inside the plant was defined by the axis order: the stem corresponds to the first axis order or order 1. The principal branches developed from the stem were of order 2; the ramifications developed from principal branches were of order 3, etc. The vigor indices are estimated by the allometric rate of the diametrical growth of the studied branching order (Crabbé 1987). The mean length of each branch that originated from the stem and the principal branches were measured at the proximal part, the median, and the distal end part. The internode length at the distal end part of each branch was measured with a digital caliper and the number of buds was been determined.

Statistical analysis

The statistical analysis was done with SPSS 10.0 for Windows statistical software package (SPSS Institute Inc., Chicago, Illinois). Analysis of variance was performed for the leaf elongation rate and morphological measurements. Each statistical sample for the leaf elongation rate and epinasty included 32 leaves and twelve plants for the morphological parameters. Differences were accepted as statistically significant when $p < 0.05$. Post hoc comparison was performed using the Student – Newman – Keuls (SNK) test.

Results

Effects of salinity on leaf elongation rate

Results showed that for all clones and treatments, the elongation rate increased at the same rate for the first six days of leaf growth, reaching an optimum at day 9 and then decreasing. The fact that this decrease was significantly steeper in salinized leaves is worth noting (Fig. 1). Differences have been depicted between the clones, with treatments with control plants showing the highest rate, and plants treated at 6 g/L NaCl having the lowest one. The OG clone was the most affected, yielding an elongation velocity of 1.16 mm·day⁻¹, while MA-195 and MA-104 clones under the same concentration displayed 2.27 and 2.08 mm·day⁻¹ respectively. Moreover, the control and plants subjected to 3 g/L NaCl reached their foliar adult size on the same date (day 39), while a significant leaf elongation delay was shown at 6 g/L NaCl. The MA-104 plants reached their leaf maturity at day 39 while the MA-195 and OG plants reached their foliar adult size on day 30 leading to an early leaf maturity.

Effects of salinity on leaf curvature

Minor differences in leaf petiole angles were observed among the clones in the absence of salt stress. Salt treatments increased leaf angles in all of the clones inducing leaf epinasty (i.e., leaf angle under salt-stress minus the corresponding leaf angle in control plants). There was no significant interaction between

genotypes and treatments (Table 1). The genotypic variation was not significant at 3 g/L NaCl (Fig. 2). Under 6 g/L NaCl treatment, epinasty was more pronounced since leaf angles increased in all clones. The OG and MA-195 clones exhibited the greatest epinastic curvature (19.33° and 17.56° , respectively) while MA-104 demonstrated the least one (16°). Epinasty induced by salt stress increased with duration of the stress. Data showed that for successive three-day intervals, at 6 g/L NaCl, epinasty was low at 3° (lower than 8° for all the clones) and increased reaching a maximum after 27 days of stress (Fig. 3).

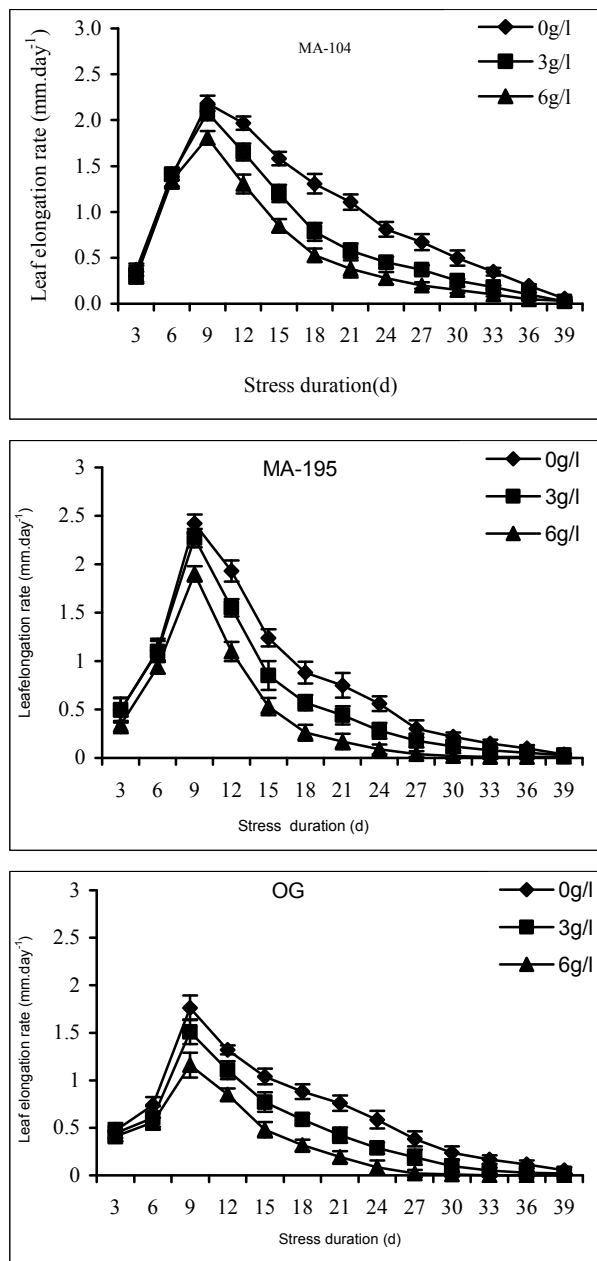


Fig. 1. Effect of sodium chloride concentrations on leaf elongation rate of the *P. alba* clones (MA-104, MA-195 and OG). The data are means values of 32 measurements and vertical bars are $LSD_{0.05}$.

Table 1. Summary of analysis of variance for different *P. alba* clones under control and salt stress conditions

Parameters	Treatment (1)	Clone (2)	(1)×(2)
	<i>p</i>	<i>p</i>	<i>p</i>
Leaf elongation	<0,0001	<0,0100	0,0062
Epinasty	<0,001	<0.03	0.3176 ^{ns}
Vigor indices	<0,0010	<0,0200	0,0408
Mean branch length	<0,0010	<0,0467	0,0252
Internode length	<0,0010	<0,0800	0,6322
Bud number	<0,0001	<0,0742	0,0375

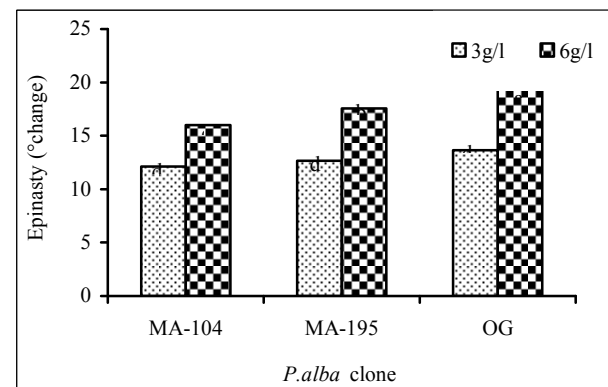


Fig. 2. Effect of sodium chloride concentration on epinasty of three *P. alba* clones. Epinasty was expressed as the difference in petiole angles between treated and control plants; thus control values are not presented in the figure. The data are means values of 32 measurements and vertical bars are $LSD_{0.05}$.

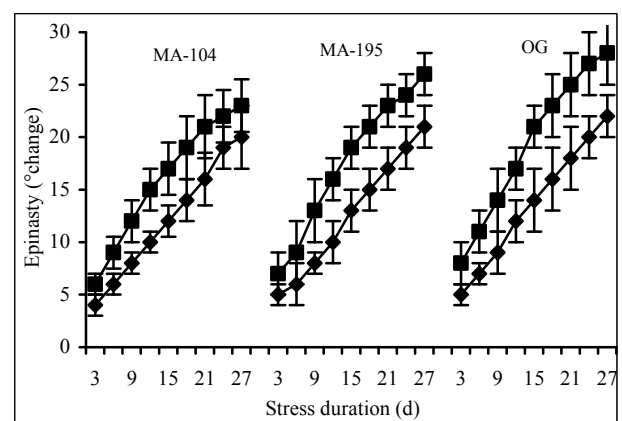


Fig. 3. Epinasty as function of sodium chloride concentrations (3 and 6g/l NaCl) and stress duration of the *P. alba* clones (MA-104, MA-195 and OG). Epinasty was expressed as the difference in petiole angles between treated and control plants; thus control values are not presented in the figure. The data are means values of 32 measurements and vertical bars are $LSD_{0.05}$.

Morphogenetic traits

Vigor analysis

The three year-old *P. alba* clones developed four axis orders: the stem corresponding to the first axis order (I) and three orders: II,

III, and IV corresponding to three levels of ramification. In the control plants, the intra and inter levels of vigor showed a gradual distribution and hierarchical organization of the ramification orders. A significant decreasing vigor gradient was obtained among the levels I and II; II and III; III and IV. It was respectively of 11%, 15% and 13% in MA-104 clone, 13%, 14% and 17% in MA-195 and 16%, 17% and 14% in OG (Fig. 4). However, the salt stress caused a significant reduction of the clone's vigor. The ANOVA showed a clone variable effect depending on the treatment used (Table 1). The treatment 3 g/L NaCl significantly reduced the vigor of MA-195 and OG clones but not of MA-104. Under 6 g/L NaCl, all clones showed a significant vigor decrease between levels (I and II), (II and III) and (III and IV) which were about 15% in MA-104 clone, 9%, 10% and 32% in MA-195 and 10%, 26% and 30% in OG, respectively. A low was noticed in the vigor axis order IV of MA-195 and OG clones (30% on average).

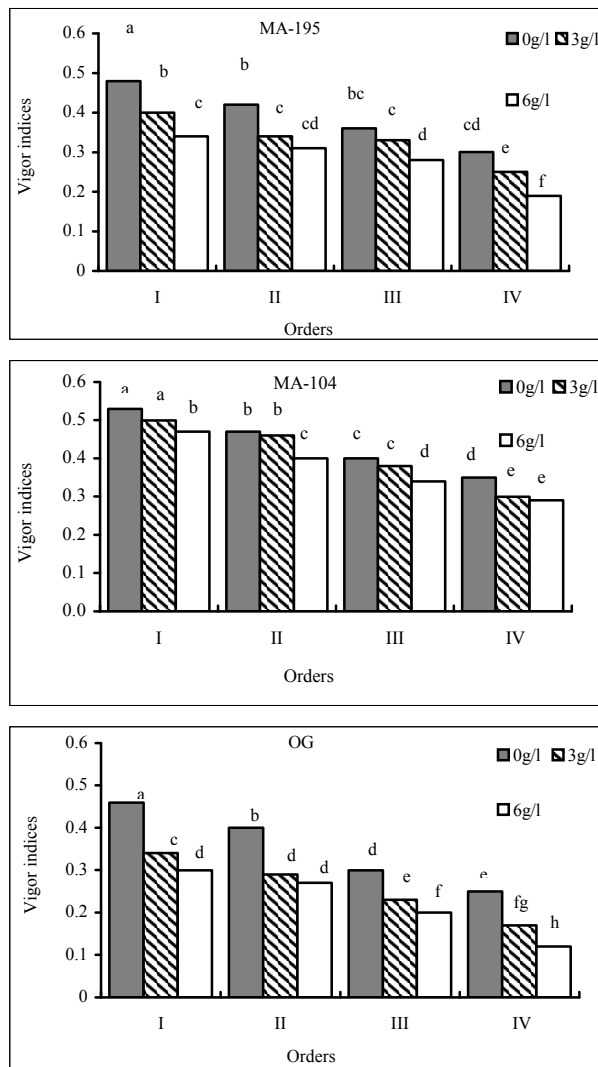


Fig. 4. Effect of sodium chloride concentration on the vigor estimation of the branching order of the three year-old *P. alba* clones (MA-104, MA-195 and OG). Values are the average of twelve plants. The data are means values of 32 measurements and vertical bars are $LSD_{0.05}$.

Length of branches

Among the criteria that allowed discrimination of environmental factors on plant morphology is the length of branches. Three branch classes were distinguished: long, middle and short branch classes where the average lengths were 60 cm, 30–60 cm, and lower than 30 cm, respectively. The frequency levels showed a dominance of the short branches (69%) compared to middle and long ones (17% and 13% respectively) (Fig. 5). The salt stress increased the number of short branches in the *P. alba* clones (Table 2). There was significant interaction between the clone and treatments. Under the level 3 g/L NaCl, no significant differences in short branch numbers were observed among the clones, while at 6 g/L NaCl, it increased in all the clones. This number ranged from OG clone which exhibited the greatest number of short branches (+33% of control) to MA-104 (+11% of control). The MA-195 clone was intermediate in short branches response (+29% of control).

Table 2. Effect of sodium chloride concentration on the short branch number, the internode length (mm) and the bud number of the three year-old *P. alba* clones (MA-104, MA-195 and OG)

Clone	NaCl (g/L)	Short branch**	Intern. length*	Bud number**
MA-104	0	17 ^{cd}	10.61 ^a	29 ^d
	3	19 ^c	9.55 ^{ab}	30 ^d
	6	19 ^c	9.14 ^b	33 ^c
MA-195	0	17 ^{cd}	14.16 ^a	32 ^{cd}
	3	19 ^c	11.7 ^b	41 ^b
	6	24 ^{ab}	8.47 ^c	46 ^a
OG	0	18 ^c	12.11 ^a	30 ^d
	3	24 ^{ab}	9.28 ^b	34 ^c
	6	27 ^a	6.97 ^c	48 ^a

The values are the average of twelve plants

*For each clone values followed by the same letter do not differ significantly according to the Student-Newman-Keuls test ($p \leq 0.05$.)

** Values in the line followed by the same letter do not differ significantly according to the Student-Newman-Keuls test ($p \leq 0.05$)

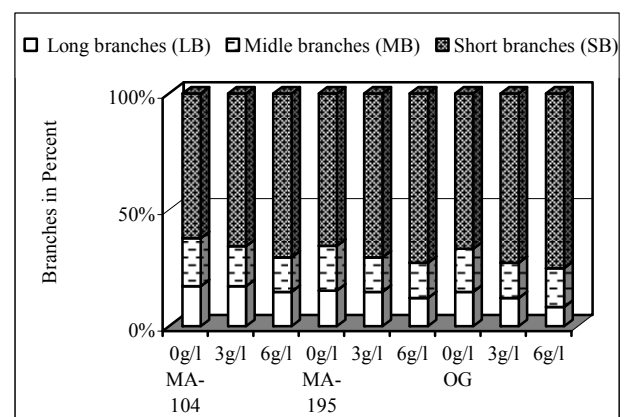


Fig. 5. Effects of sodium chloride on the percentage of long, middle and short branches' number of the three year-old *P. alba* clones (MA-104, MA-195 and OG).

Moreover, the effect of salinity treatments significantly reduced the internode length (Table 2), with no significant interaction occurring between clones and treatments. The salt treatment (3 g/L NaCl) caused minimal reduction on the internode length of the MA-104 clone but significant decreases were noted on MA-195 and OG (-20% and -23% of control), respectively. At 6 g/L NaCl, significant internode shortening was noted. By comparison to the control, this reduction was of 13%, 40% and 42% in MA-104, MA-195 and OG, respectively.

The salt level (6 g/L NaCl) caused a significant increase in the bud numbers in the *P. alba* clones. The OG showed the greatest increase (+38% of control) by contrast to the MA-104, which demonstrated the least (+12% of control). The MA-195 clone demonstrated an intermediate response (+30% of control).

The morphological observations showed that salt stress stimulated the production of floral buds on *P. alba* plants in comparison to control that presented vegetative buds (Fig. 6). Hence, floral stimulation was sensitive to the salinity level. At 3 g/L NaCl, floral bud production was stimulated in the OG and MA-195 clones, which was not the case of MA-104 (Fig. 6). At 6 g/L NaCl, it was much more prominent in OG and MA-195 but was less important in MA-104. Meanwhile, the toxic effect of salinity, especially at the level 6 g/L NaCl, caused necrosis and abscission of leaves. These effects ranged from OG, which was severely affected by leaf abscission and most of its leaf surface was necrotic, to MA-104 associated with minor differences with control. The MA-195 clone was intermediate in necrosis and leaf abscission responses.

Discussion

Clones of Tunisian *P. alba* genotypes showed differential morphological responses to long-term salt stress under semi-controlled conditions. Our results showed the tolerance of such clones to the moderate level of salinity (3 g/L NaCl) confirms that *P. alba* is a species with an intermediate degree of salinity tolerance (Beritognolo et al. 2007). The clones, however, displayed differential behaviour in response to a higher level of salinity (6 g/L NaCl). The OG and MA-104 were the most and least susceptible clones respectively. These results are consistent with earlier observations (Abassi et al. 2010) on the impact of this level of salinity on the biomass growth of 1-year-old *P. alba* genotypes. Results showed that the responses of *P. alba* clones to salinity stress included a marked decrease in leaf elongation rate, leaf epinasty, and a general inhibition of growth leading to a loss of vigour, plant architectural modification, and early tree maturation.

These responses depended on the degree of tolerance of the *P. alba* genotypes to salinity. The delay noticed in leaf elongation rate (Fig. 1) might be caused by decreased turgor pressure (Bouchabke et al. 2006) or by rigidity of the cell walls resulting from osmotic stress (Cosgrove 2005). The sensitivity of the OG and MA-195 clones to the level 6 g/L NaCl was demonstrated by cessation of leaf elongation leading to an early leaf maturity. A

similar effect was observed on rice species subjected to water stress (Tanguilic et al. 1987). By comparison, early leaf maturity developed by the OG and MA-195 clones could be a way to avoid lack of energy induced by salt stress.

The exposure of *P. alba* clones to salt stress was accompanied by epinastic growth of petioles, the magnitude of which was increased by stress severity (Fig. 2). Petiolar epinasty induced by salt stress is generally related to an increase in ethylene synthesis within the aerial plant parts (El Iklil et al. 2000, Munns and Tester 2008). Results showed that the incremental responses of individual petioles at the highest salinity concentration (6 g/L NaCl) were highly dependent upon the genotype. Petiolar angle in treated, sensitive OG plants increased nearly 2 times over that observed in the controls. While in the tolerant MA-104 clone, increase in the petiolar angle was of 1.6 times the controls. These findings are consistent with earlier research stating that salt-induced leaf epinasty is a sensitive indicator of salt tolerance (Jones and El-Beltagy 1989; El-Eklil et al. 2000). Moreover, epinasty increase with duration of stress was genotype dependent (Fig. 3). In the highly responsive MA-104 clone, petiolar angle increased nearly 1.5 fold while the least responsive clone (OG) exhibited a 3.5 fold increase.

The architectural observations showed that the three -year-old *P. alba* clones developed four axis orders. The salt stress affected tree development, inducing loss of vigour, for which the magnitude was most prominent at 6 g/L NaCl. The *P. alba* clones displayed intra- and inter-specific variability in response to their tolerance to salt treatment. The vigour of OG and MA-195 were seriously damaged, while the MA-104 clone demonstrated less vulnerability (Fig. 4). The branching traits showed that independently of the salt stress, the *P. alba* clones developed a high percentage of short branches which could be the species' morphogenetic characteristics. The moderate tolerance to high levels of salinity of the *P. alba* clones (Beritognolo et al. 2007) was demonstrated by the increase in the rate of short branches and the stunting of growth induced by shortening the internode length.

These results confirmed those of Gucci et al. (1997) and Barhoumi et al. (2007) suggesting that salt stress has shortened internode length of both *Phillyrea* sp. and *Aeluropus litoralis*. Moreover, subjecting *P. alba* clones to 1–2 years of salt stress enhanced flower initiation followed by early flowering (Fig. 6). However, in natural stands, the transition to flowering in *Populus* involves multiple protracted temporal and spatial components (Brunner and Nilsson 2004) and poplar requires between five and seven years to become sexually mature (Braatne et al. 1996). Salt stress is capable of inducing an abbreviated transition between the juvenile and mature phases, an adaptation mechanism developed by *P. alba* clones. In this context, Greenwood (1995) stated that the earliest maturation event in conifers is a change in meristematic behaviour, losing regenerative potential and capacity for vegetative growth to gain reproductive competence and more massive leaves, which are better adapted to the increasing environmental stresses.

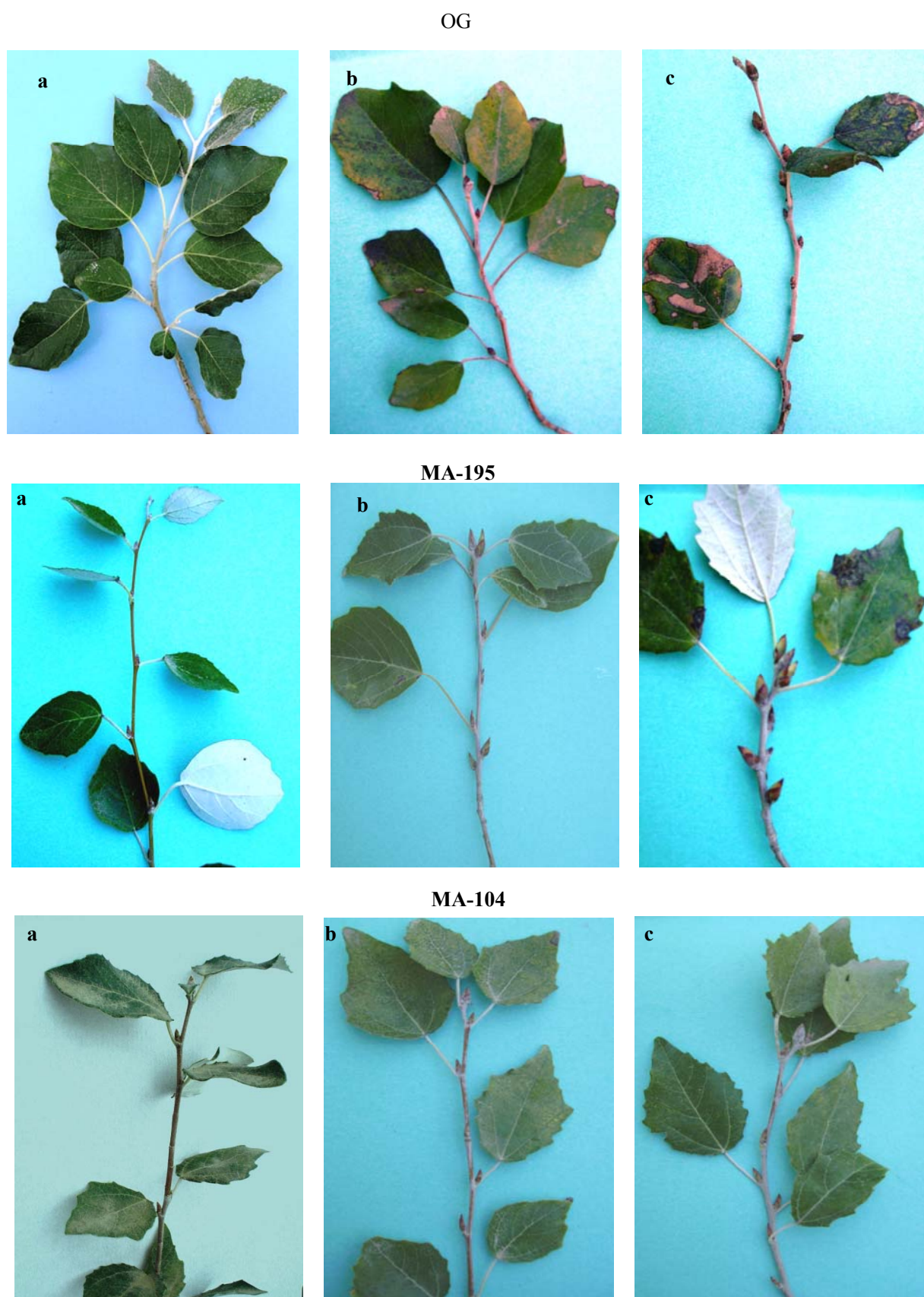


Fig. 6. Effect of salt stress on leaves and buds of *P.alba* clones (MA-104,MA-195 and OG) . (a: control, b: plants subjected to 3g/L NaCl, c: plants subjected to 6 g/L NaCl).

Because salinity induces multiple stresses on the plant, including osmotic imbalance, nutritional deficits, and cellular toxicity (Parida et al. 2005), it is difficult to identify the specific mechanisms behind the flowering in *P. alba* clones. One potentially important factor enhancing flower initiation in *P. alba* clones could be the reduced root biomass, which decreases energy reserves that impede vegetative growth and stimulate reproduction (Abassi et al. 2010). Our observations (Fig. 6) attested to the sensitivity of the OG clone to a high level of salinity. In this context, leaf senescence and leaf necrosis demonstrated OG clone sensitivity to the level 6 g/L NaCl, while the most responsive MA-104 clone survived without showing drastic symptoms. Leaf necrosis could be related to the high uptake of chloride in the OG clone (Abassi 2009).

In conclusion, *P. alba* clones showed no symptoms at 3 g/L NaCl, confirming their tolerance to this moderate level of salinity. They showed variable behaviour when subjected to higher saline treatment (6 g/L), attesting to the tolerance of the MA-104 clone. Different strategies for adaptation to long-term salt stress have been observed, including change in the morphological status and shorter growth cycle. This behavior demonstrates the elasticity and ease of accommodation under salt stress. However, considering the variability in salinity tolerance observed in the clones studied, we recommend continuing these studies, with the goal of exploring the clones' adaptive variability in view of existing physiological criteria, such as water relations and mineral uptake.

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